# Rival group scent induces changes in dwarf mongoose immediate behaviour and subsequent movement

**Charlotte Christensen[1*], Julie M. Kern[1], Emily Bennitt[2], Andrew N. Radford[1]**

[1]*School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, United Kingdom*

[2]*Okavango Research Institute, University of Botswana, Maun, Botswana*

*Correspondence: cc0157@bristol.ac.uk

Running headline: Territorial responses to rival group scents

**In many social species, groups of animals defend a shared territory against rival conspecifics. Intruders can be detected from a variety of cues, including faecal deposits, and the strength of response is expected to vary depending on the identity of the rival group. Previous studies examining differences in response to neighbour and stranger groups have focused on the immediate response to the relevant cues. Here, we investigated how simulated intrusions of rival groups affect both immediate responses and post-inspection movement patterns. To do so, we used a faecal translocation experiment at latrine sites within the territories of dwarf mongoose *Helogale parvula* groups. Immediate responses were adjusted to the level of threat, with greater scent-marking behaviour, time spent at the latrine and group-member participation when groups were presented with faecal matter from out-group rivals relative to control (own-group and herbivore) faeces. Subsequent movement of the group was also affected by threat level, with a decrease in speed and distance covered following simulated intrusions by out-group rivals compared to control conditions. However, there were no significant differences in immediate responses or post-latrine movement patterns when comparing simulated neighbour and stranger intrusions. These results indicate that territorial intrusions can elicit not just an immediate change in behaviour but more far-reaching consequences in terms of movement dynamics. They also raise the possibility that neighbour–stranger discrimination predictions are not necessarily as clear-cut as previously described.**

Keywords: group identity; identity cues; latrine behaviour; out-group conflict; social behaviour; territory defence

## 1. Introduction

In many social species across a range of animal taxa, individuals form stable groups that collectively defend a territory against conspecifics (Taborsky 1984; Radford 2003; Kitchen and Beehner 2007; Batchelor and Briffa 2011). The level of threat posed by rival groups is likely dependent on several factors. For instance, the territorial location can be important, with intruders nearer the centre than the periphery or those close to particularly valuable resources perceived as a greater threat (Furrer et al. 2011; Brown 2013). Relative resource-holding potential can also have an influence, with larger groups tending to dominate smaller ones in inter-group conflicts (McComb et al. 1994; Radford and du Plessis 2004). Moreover, intruder identity can affect the degree of threat, with differences in response to neighbours and strangers found in a number of taxa (Temeles 1994).

The "dear enemy phenomenon" (Fisher 1954), where residents show less aggressive responses to intruding neighbours compared to strangers, is found in some group-living species such as green woodhoopoes *Phoeniculus purpureus* (Radford 2005). In general, neighbours might be less threatening than strangers either because they are known to be continuously present at a mutual border, whereas intrusions by strangers are spatially and temporally unpredictable (Jordan et al. 2007), or because they already own a territory, whereas transient strangers may be looking to usurp residents and take over (Wilson 1980). The "nasty-neighbour phenomenon" (Müller and Manser 2007), where intrusions by neighbours are countered with higher levels of aggression than those by strangers, is found in other group-living species such as banded mongooses *Mungos mungo*, where emigration from the natal territory is undertaken in small groups (Müller and Manser 2007). Small stranger groups pose less threat to established residents than large neighbouring groups both in terms of size and intention: stranger groups might simply be passing through, while neighbours could be seeking to expand their territory (Mech and Boitani 2003; Müller and Manser 2007).

Neighbour–Stranger discrimination (NSD) has been shown to be possible through vocal, visual and olfactory cues. Resident green woodhoopoes responded significantly more rapidly to playbacks of strangers (posing the threat of permanent territorial eviction) than of neighbours (causing temporary displacements) (Radford 2005), while other species even discriminate between different neighbouring groups on the basis of their vocalisations (e.g.

vervet monkeys *Cercopithecus aethiops*, Cheney and Seyfarth 1980; chimpanzees *Pan troglodytes*, Crockford et al. 2004). In Jacky dragons *Amphibolurus muricatus*, static presentations of unfamiliar individuals elicited significantly higher levels of arousal and signs of information gathering than familiar individuals, supporting dear-enemy predictions (Husak 2004; Van Dyk and Evans 2007). Eurasian beavers *Castor fiber*, European badgers *Meles meles* and African wild dogs *Lycaon pictus* all responded more intensely to scent-marks from strangers than to those from neighbours (Rosell 2001; Palphramand and White 2007; Parker 2010), while banded mongooses responded more strongly when encountering the scent of a neighbour than of a stranger group (Müller and Manser 2007).

To date, studies of how residents respond to intruder scent-marks have focussed on the immediate behavioural responses. Inspection, over-marking (i.e. depositing own scent over the encountered scent) and physical displacement or destruction of the scent-mark, as well as the number of individuals participating and vocalisations given to recruit other group members, have all been shown to vary depending on the level of perceived threat (Roper et al. 1993; Rosell 2001; Müller and Manser 2007; Mares et al. 2011). However, the discovery of intruder scent-marks might also be expected to influence subsequent behaviour, as is the case following actual encounters between rival groups. For instance, white-faced capuchin monkeys *Cebus capucinus* travelled further, faster and more linearly if a conflict was lost (Crofoot 2013); increased speed incurs energetic costs and faster travel means a smaller likelihood of detecting food (Janson and Di Bitetti 1997) and less time spent resting (Dunbar and Dunbar 1988). Straight-line movement has been associated with flight (e.g. coyotes *Canis latrans*, Neale et al. 2007), while increased tortuosity could indicate a search pattern (e.g. Weddell's saddleback tamarins *Saguinus fuscicollis weddelli*, Porter and Garber 2013). Territory exploration (visiting sleeping burrows) after the detection of a transient group scent-mark has been noted in meerkats *Suricata suricatta* (Jordan et al. 2007), but movement patterns after the detection of intruder scent-marks has yet to be addressed experimentally in a group-living species.

In this study, we use dwarf mongooses *Helogale parvula* to investigate immediate and longer term responses to simulated territorial intrusions (faeces placed within the focal territory) by rival conspecific groups. Dwarf mongooses live in cooperatively breeding groups with a dominant breeding pair; group members sleep, forage and travel together within a shared territory (Rood 1983; Kern and Radford 2013). Cooperative territorial behaviour involves

129 scent-marking at communal latrines and physical defence when other groups are encountered
130 (Rasa 1973). Four olfactory channels are used: urine, faecal matter and both cheek-gland and
131 anal-gland secretions (Rasa 1973). In a captive setting, the introduction of faecal matter from
132 an unfamiliar pair resulted in increased anal-gland marking by a focal pair compared to when
133 their own faecal matter was present (Rasa 1973). Recent findings in the field suggest that no
134 discrimination is made between stranger and own faecal matter when single faeces are
135 presented alongside one another (Sharpe 2015). However, latrines in the wild are usually
136 frequented as a group and scent-marks are deposited by multiple group members at such sites
137 (Sharpe et al. 2012), likely resulting in a group signature (Ewer 1968; Rasa 1973). We
138 therefore investigated group-level responses to out-group threats as indicated by faeces from
139 several individuals.
140
141 Our faecal-presentation experiment, considering both immediate behavioural interactions
142 with the presented faeces and subsequent movement patterns by the territory-holding group,
143 aimed to answer two main questions. First, do territory holders respond more strongly to
144 faeces from other groups (out-group threat) than to control faeces (those from their own
145 group and from herbivores)? Since out-group faeces will be less familiar to individuals than
146 those from their own group, and out-groups represent a potential threat in terms of resource
147 loss and territory usurpation, we predicted a stronger response to faeces from rival groups
148 compared to control faeces. Second, do territory holders respond differentially to faeces from
149 neighbours and strangers? Neighbouring dwarf mongoose groups commonly contest the
150 temporary rights to sleeping burrows on the mutual boundary of their territory, while conflict
151 with transient groups rarely involves sleeping-site contestation and are generally less intense
152 (Rasa 1987). The majority of observed intergroup interactions take place between
153 neighbouring groups (unpublished data) and repeated intrusions intensify responses to rivals
154 in other species (Monclús et al. 2014). We therefore predicted a stronger response to faeces
155 from neighbours than to those from strangers.
156

157 ## 2. Material and methods

158 ### (a) Study site and population

159 The study was conducted on Sorabi Rock Lodge, a 4 $km^2$ private reserve in the Limpopo
160 Province, South Africa (24° 11'S, 30° 46'E), part of southern Africa's Savannah Biome (see
161 Kern and Radford 2013 for full details). We collected data over two periods: November 2013

to January 2014 (summer) and June 2014 to October 2014 (winter). All procedures were approved by the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UB11/038).

The long-term study population consists of eight groups of dwarf mongooses (group sizes ranging from 3 to 15 individuals), habituated to close human presence on foot and thus allowing for detailed observation (<5 m) in natural conditions (Kern and Radford 2013, 2014). Individuals can be identified from marks of blond hair-dye (Garnier Nutrisse) applied using an elongated paint-brush whilst distracting the mongoose with egg. Dominant individuals are recognised by their higher levels of aggression, feeding displacement and greeting behaviours (Rasa 1977; Kern et al. 2016). Groups are visited regularly to maintain habituation, re-apply hair-dye, collect baseline data and keep track of important life-history events (e.g. pregnancies, births, emigration, dominance changes and deaths).

## (b) Experimental protocol

The experiment aimed to investigate differences in both immediate behavioural responses and subsequent movement patterns following four different faecal presentations. The four treatments comprised faeces collected from: a neighbouring group (Neighbour), a non-neighbouring group (Stranger), the focal group (Own) and a herbivore (Herbivore). Own and Herbivore represent two forms of control: Own controlled for the presence of conspecific faecal matter, which might be expected to result in some responses due to intra-group non-territorial functions (Rasa 1973; Sharpe 2015); and Herbivore controlled for the interference by the experimenter with the latrine and the addition of faeces. We presented treatments to the same group on different days in a randomised order; subsequent analysis confirmed that there was no unintentional bias in the ordering of different treatments (Friedman test: $\chi^2$=2.35, n=13, p=0.502).

To standardise between the different mongoose faecal treatments (Own, Neighbour, Stranger), each presented sample consisted of one faeces from each of four separate group members, including at least one of the dominant pair. For the Herbivore treatment, we used four faecal pellets from greater kudu *Tragelaphus strepsiceros* or giraffe *Giraffa camelopardalis* (diameter ~2 cm; same size as dwarf mongoose faeces). Faeces were

collected within 5 min of deposition, placed in airtight, sealed plastic bags inside glass pots while in the field, and stored overnight in a fridge (5°C). Faeces were always used in an experimental presentation within 1 day of collection (mean±SE=13.0±1.6 h), and there was no significant difference between treatments in time between collection and use (Friedman test: $\chi^2$=1.92, n=13, p=0.584).

We conducted faecal presentations at mongoose latrines, which are communal, frequently used elimination sites. Latrines are recognisable by the accumulation of faecal matter (Rasa 1973) and their location was marked using handheld GPS devices (Garmin Etrex H GPS; Garmin Europe Ltd., Southampton, Hampshire, UK) during observational data-collection sessions. After the focal group left their sleeping burrow, the observer tracked the presence of nearby latrines using the GPS map while following the foraging group. If the group was approaching a latrine (within 15 m), the observer moved ahead quietly and placed the faecal presentation on the ground at that site, before moving 5 m away; this distance allowed detailed observations without affecting latrine activity by the mongooses. We did not conduct faecal presentations if there had been an inter-group interaction earlier in the day; at least 30 min were allowed to elapse since any other latrine activity before faeces were presented in an experimental trial.

### (c) Data collection

We defined the start of the focal-group response as the first interaction (sniffing) with the faecal presentation by any group member. Thereafter, we recorded the following data: number and identity of individuals present at the latrine (every 30 s); the total time spent at the latrine by all responders; and the latrine behaviours exhibited (sniffing, urinating, defecating, cheek-gland marking and anal-gland marking by hand-standing) by all responders. Cheek-gland marking involves rubbing the corners of both cheeks alternately against a surface, is predominantly performed by dominant individuals, and is considered a display of aggression. Anal-gland marking is performed by everting the anal gland pouch containing anogenital secretions; adopting a “handstand” position, balancing on the forelegs and swinging the back legs up to mark sloping surfaces, allows individuals to deposit the scent at an elevated level (Rasa 1973; Estes 1999). We gave each latrine behaviour in the 15 min following the first interaction with the faecal presentation a score, based on its rank inferred from assumed energy-investment and importance in territorial defence; anal-gland

marking by hand-standing is considered the most energetically costly scent-marking behaviour (Sharpe et al. 2012): sniffing=1, urinating=2, defecating=3, cheek-gland marking=4, anal-gland marking=5. We summed scores to generate a "response level" value for the group.

We collected continuous movement data (track position recorded every 10 s) using a GPS for the hour after the interaction with the faecal presentation. We imported data via Basecamp (software version 4.4.6, Garmin Ltd.) into Mapsource (software version 6.16.3, Garmin Ltd) and stored them as daily movement maps. From these maps, the distance travelled, time of travel, average speed and the area covered by the track were calculated automatically. To infer "directness" of travel, we calculated circuity indexes by dividing the track distance by the direct distance between the location of the faecal presentation and the location of the group one hour after the first interaction (Janson 1998; Porter and Garber 2013).

**(d) Assignment of latrine locations**

While the initial aim was to conduct all faecal presentations in the periphery of the territory—territory location is known to influence the response to intruders in other group-living species (Furrer et al. 2011; Brown 2013)—this was precluded by the limited range used by our study population during the data-collection period in the second field season. To classify each experimental latrine site as either core or periphery, we calculated home ranges using the movement data collected over the six months preceding the relevant experimental field season. In the two instances where prior movement data did not extend back six months, we used all available data (three months in both cases). Six months was chosen as a balance between including sufficient data (mean±SE observation sessions=50.5±3.8; mean±SE geographical data points=480±60) and delineating a plausible home range, as space use varies over time (unpub. data). We transferred the geographical waypoint data from the daily movement maps for each group during each period into Mapsource (as above) and then into QGIS (version 2.6.1 Brighton, FOSS). Using the Minimum Convex Polygon (MCP) algorithm from the plugin AniMove (version 6.16.14, Garmin corp), we calculated MCPs using 100% of the data point fixes to estimate the full home-range (as in Gilchrist and Otali 2002; Mattisson et al. 2013). Subsequently, the central 50% fixes were used to determine which latrines were classified as core (within MCP 50) and which as peripheral (outside MCP 50) (as in José and Lovari 1998; Jędrzejewski et al. 2007).

## (e) Data analysis

We analysed data using R version 3.1.2 (R Development Core Team 2012). We used mixed models to take account of repeated data from the same group. Linear Mixed Models (LMMs) were used throughout since datasets, or their log or square-rooted transformations, fit the assumptions of parametric testing. We added treatment (Neighbour, Stranger, Own, Herbivore), territorial location (Core, Periphery), pup presence (Yes, No) and time of day (AM, PM) as fixed effects. Pup presence was defined as the period of time after birth until the pups are observed to first forage independently (~1 month). We added group ID as a random factor. The minimal model was determined by calculating the change in deviance during step-wise removal of fixed effects. Additionally, Akaike Information Criterion (AIC) values for each model were considered (Akaike 1974); lower AIC values represent a better fit and corresponded to the minimal model acquired on deviance change grounds. When treatment was found to have a significant overall effect, we conducted three planned contrasts for each relevant response variable. First, we compared Herbivore and Own to test for any difference between control treatments. Since these were never found to differ significantly (see Results), we tested for an effect of out-group threat (Neighbour and Stranger combined) versus non-threat conditions (Herbivore and Own combined). Finally, we tested for a difference in response between the two out-group threats (Neighbour versus Stranger).

The aim was to conduct full sets of trials (all four treatments) at each group of the two data-collection periods. However, two groups from the first data-collection period were excluded from the analyses as not all the trials were completed. More than 40% of group members changed between the two study periods (separated by 9 months) in five of the six remaining groups with completed datasets for the first period; group compositions from the middle date in each experimental set were compared. Thus, we treated them as different groups in the analyses; data from only one run of the experiment were included from the remaining group to avoid pseudo-replication. Thirteen complete sets of trials were therefore included in the analyses of immediate responses. For the movement data, only the eight groups from the second field season were available, due to incomplete track data in the first field season.

## 3. Results

### (a) Immediate behavioural responses

Experimental treatment had a significant effect on the overall response level to the presented faeces (Table 1a), time spent at the latrine by group members (Table 1b) and the proportion of the group participating in the latrine activity (Table 1c).

For all three response variables, there was no significant difference between the two control treatments (Herbivore versus Own): response level (planned contrast: $Z=1.54$, $p=0.326$; effect size±SE=2.08±1.35); time spent ($Z=0.58$, $p=0.916$; effect size±SE=0.08±0.14); proportion of group participating ($Z=1.04$, $p=0.654$; effect size±SE=0.07±0.07). However, there was a significantly stronger response to out-group threats than to non-threat treatments. Focal groups exhibited a higher response level ($Z=2.74$, $p=0.020$; effect size±SE=2.58±0.95; Figure 1a), spent longer at the latrine ($Z=3.07$, $p=0.006$; effect size±SE=0.30±0.10; Figure 1b) and had more members participating in the latrine activity ($Z=3.17$, $p=0.005$; effect size±SE=0.16±0.05; Figure 1c) when presented with out-group faeces compared to control faeces.

Responses did not differ significantly depending on the identity of the out-group threat. There was no significant difference in response intensity (planned contrast: $Z=0.46$, $p=0.956$; effect size±SE=0.62±1.35), time spent at the latrine ($Z=1.05$, $p=0.650$; effect size±SE=0.15±0.15) or proportion of the group participating in the latrine activity ($Z=0.41$, $p=0.968$; effect size±SE=0.03±0.07) when groups were presented with Neighbour versus Stranger faeces.

### (b) Movement responses

After controlling for a significant positive influence of pup presence, experimental treatment had a significant effect on the travel speed of groups (Table 2a) and the distance travelled by the group (Table 2b) in the aftermath of faecal presentations. Treatment did not have a significant effect on the direct distance travelled (Table 2c), travel circuity (Table 2d) or the area covered (Table 2e) in the hour after interaction with the faeces.

There was no significant difference between the two control treatments (Herbivore versus Own) in either travel speed (planned contrast: $Z=1.57$, $p=0.306$; effect size±SE=0.12±0.08) or distance travelled ($Z=1.39$, $p=0.418$; effect size±SE=2.79±2.01). However, there was a

significantly stronger response to out-group threats than to non-threat treatments. Focal groups travelled slower ($Z=3.59$, $p=0.001$; effect size±SE=0.19±0.05; Figure 2a) and covered less distance ($Z=3.20$, $p=0.004$; effect size±SE=4.63±1.45; Figure 2b) following interactions with out-group faeces compared to control faeces.

Responses did not differ significantly depending on the identity of the out-group threat. There was no significant difference in travel speed (planned contrast: $Z=0.76$, $p=0.833$; effect size±SE=0.06±0.08) or in distance covered ($Z=0.89$, $p=0.755$; effect size±SE=1.85±2.09) by groups following presentations of Neighbour and Stranger faeces.

## 4. Discussion

### (a) Threatening vs. non-threatening context

Our results show that, as predicted, dwarf mongooses respond strongly to faeces from rival groups both in terms of immediate behavioural interactions at the latrine and in subsequent movement patterns. The larger proportion of the group participating in response to faeces indicating a territorial threat compared to control conditions corresponds to findings in banded mongooses and meerkats, where individuals encountering latrines containing recent evidence of out-group activity vocalise to recruit other group members (Müller and Manser 2007; Mares et al. 2011). Since relative group size influences contest outcomes in many group-living species, with larger groups tending to win (McComb et al. 1994; Cant et al. 2002; Radford and du Plessis 2004), increased participation from group members in latrine activity may be an attempt to signal resource-holding potential to the intruding group were they to return to that latrine. The increase in time investment during latrine activity in threatening contexts may indicate a larger interest in the presented scent (Müller and Manser 2007; Mares et al. 2011; Sharpe 2015) or a longer time spent by individuals in depositing their own scent. Either way, it is time invested in territorial defence, which is not invested elsewhere (Nolet and Rosell 1994).

Our finding of a stronger immediate response to out-group faeces compared to own-group faeces contrasts recent work by Sharpe (2015), who found no significant difference in the time individual dwarf mongooses spent inspecting individual faecal samples from different groups (Sharpe 2015). However, our experiment differed from that previous study in a number of potentially crucial aspects. First, we considered group-level responses, whereas

Sharpe (2015) investigated the behaviour of a single mongoose. Group members are likely to vary in how threatened they are by out-group individuals and some may not respond particularly strongly to them (Desjardins et al. 2008; Mares et al. 2011; Bruintjes et al. 2016). Second, we presented faeces from multiple individuals from a group, rather than faeces from a single individual. Intruding groups and individuals pose potentially very different threats: rival groups may be looking to annexe territorial space (Wilson and Wrangham 2003; Kitchen and Beehner 2007; Golabek et al. 2012), whereas individuals may be seeking reproductive opportunities or dominance positions (Mares et al. 2011; Bruintjes et al. 2016). Finally, whereas Sharpe (2015) presented all faecal treatments simultaneously at the same latrine, we presented our treatments at separate times at different latrines since it is unlikely that all would be naturally encountered together. The stronger response to out-group faeces compared to control faeces in our experiment suggests that scents of rival groups are threatening and that dwarf mongoose faeces do provide some information about group identity.

The slower movement of dwarf mongoose groups, and the shorter distance they covered, after encountering evidence of a territorial threat (faeces from rival groups) is in line with findings in solitary southern hairy-nosed wombats *Lasiorhinus latifrons* (Descovich et al. 2012). After encountering faecal samples from conspecific males, individual male wombats moved less as a consequence of increases in vigilance and hiding behaviour (Descovich et al. 2012). Male red foxes *Vulpes vulpes* did not decrease their speed, nor did they travel a shorter distance after artificial urine scent-marks were placed within their territory, but a significantly higher proportion of time was spent patrolling the scent-marked area, suggesting a motivation to reclaim that part of the territory (Arnold, Soulsbury and Harris 2011). Although we did not record the specific behaviour of dwarf mongooses in the hour after faecal presentations, it is plausible that slower-moving groups may be more vigilant. This has been shown in the context of predator detection, where slower movement, with intermittent pausing, increases the likelihood of detecting danger (McAdam and Kramer 1998). The dwarf mongooses might therefore have moved slower in an attempt to detect intruders in the vicinity of the latrine, resulting in a shorter distance travelled. Moreover, although no significant difference was found between direct distances from the latrine to the end point an hour later, slower movement may result in more time being spent in the intruded area, asserting the presence of the group as part of a territorial defence strategy. Claiming an area in the aftermath of a contest has been demonstrated in roost selection in green woodhoopoes, where groups will

arrive earlier at the roost after conflict as a means of securing the resource from the neighbouring group (Radford and Fawcett 2014).

### (b) Neighbour vs. stranger context

Our experiment provided no evidence for a difference in response to neighbour and stranger faeces in either immediate behaviour or in post-latrine movement. One theoretical reason for the similar responses is that Neighbour–Stranger discrimination (NSD) is simply not possible from the presented cues. However, previous work on dwarf mongooses has suggested that the deposition of scent-marks by multiple individuals may result in a group signature (Ewer 1968; Rasa 1973), so the relevant information is likely available. Another theoretical reason is that discrimination is possible, but that there has been no selection for a differential response, as has been shown in other contexts and species (e.g. meerkat use of alarm calls; Schibler and Manser 2007). However, NSD appears adaptive in many other species (see Introduction) and there are no obvious reasons why dwarf mongooses should be different in this regard. Instead, a lack of apparent NSD may arise for two main reasons (see also Frommolt et al. 2003; Battiston et al. 2015).

First, the relative threat posed by neighbours and strangers, rather than being fixed, may fluctuate depending on contextual factors and relative protagonist characteristics. For instance, neighbours may have different resource-holding potential depending on their group size (McComb et al. 1994; Cant et al. 2002; Radford and du Plessis 2004), and previous encounters may determine the nature of the relationship (Müller and Manser 2007; Zenuto 2010; Monclús et al. 2014), with the level of aggression shown by particular neighbours affecting the reaction to them (Hyman and Hughes 2006). Another potential influencing factor is the proportion of borders shared by neighbouring groups. In our population, central groups whose territories are surrounded by several others may receive more neighbour pressure than peripheral groups located, for instance, next to the main road. A third possibility might be that the relative threat from neighbours and strangers changes with season; for example, the proximity of neighbours may be viewed as a greater threat when groups have vulnerable young (Temeles 1994; Briefer et al. 2008). In dwarf mongooses, a general increase in scent-marking occurs days prior to the birth of a litter and during the babysitting period (Rasa 1973). Having dependent pups, when intrusions by neighbours can lead to infanticide, could conceivably result in nasty-neighbour relations during the breeding

425 season, but a dear-enemy effect at other times of the year. These possible drivers of identity-
426 dependent responses to out-groups remain to be explored.
427
428 A second general explanation for the lack of a difference in response to neighbour and
429 stranger faeces is that responses to intruder scent may be dependent on the identity of the
430 particular individuals who deposit and receive the signal. We considered responses from a
431 group-defence perspective, but that entails the actions of multiple individuals who do not all
432 have the same interests and motivations (Olson 1971; Radford 2004; Crofoot et al. 2008;
433 Crofoot and Gilby 2012). For instance, a link exists between scent-marking and status, with
434 dominant males in particular often contributing more than other group members either
435 because they have a higher interest in territory defence and/or mate-guarding than
436 subordinates (Johnson 1973) or because their better body condition allows greater investment
437 (Gosling and Roberts 2011). Sex of the intruder may also affect the response depending on
438 the sex of the receiver, particularly during the mating season (Roper et al. 1986; Mares et al.
439 2011) as males and females may be signalling different messages (Wronski et al. 2013).
440 Despite reproductive skew in dwarf mongooses, all group members participate in territorial
441 scent-marking and, unlike other species, both sexes perform handstands (Sharpe et al. 2012).
442 However, it is conceivable that some experimental trials involved higher attendance of, for
443 instance, dominant males, producing overall higher response levels than those that did not,
444 potentially masking NSD.
445
446 **(c) Conclusions**
447 While previous studies have demonstrated an immediate response of territorial groups to the
448 presence of out-group faeces, our work demonstrates that there can be longer-lasting effects
449 in terms of movement patterns. This could have energetic costs or consequences in terms of
450 foraging success, predation risk, selection of sleeping burrows and territory maintenance;
451 these are possibilities, with potential fitness implications, that require consideration in future
452 studies. Our work also suggests that a view of species as exhibiting either a dear-enemy
453 effect or a nasty-neighbour effect may be too simplistic. Further work is needed on social
454 species in terms of both individual contributions to territorial responses to intruders and the
455 fluctuating nature of relationships between resident groups and neighbours or strangers.
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**Data accessibility:** Data will be made available in Dryad if the paper is accepted for publication.

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## Figure legends

**Figure 1.** Response of dwarf mongoose groups to experimental presentations of threatening (Neighbour, Stranger) and non-threatening (Own, Herbivore) faeces. Shown are (a) response level (b) total time spent at the latrine and (c) proportion of the group participating for each group (n=13) separately (grey lines) and the mean response (black line).

**Figure 2.** Movement responses of dwarf mongoose groups in the hour after experimental presentations of threatening (Neighbour, Stranger) and non-threatening (Own, Herbivore) faeces. Shown are (a) speed of travel and (b) distance travelled for each group (n=8) separately (grey lines) and the mean movement response (black line).

**Table 1.** Linear Mixed Models investigating factors affecting (a) response level (raw data), (b) time at latrine (log transformed), (c) and proportion of group participating (square root transformed) following experimental faecal presentations.

| | $\chi^2$ | *Df* | *P* | *AIC* |
|---|---|---|---|---|
| **(a) Response level** | | | | |
| **Treatment** | **8.82** | **1** | **0.032** | **297.180** |
| Territory location | 0.83 | 1 | 0.363 | 298.353 |
| Pup presence | 1.47 | 1 | 0.225 | 297.709 |
| Time of day | <0.001 | 1 | 0.980 | 299.179 |
| | | *Effect Size* | *SE* | |
| Constant | | 5.92 | 1.11 | |
| Group ID | | 1.75 | 3.44 | |
| **(b) Time** | | | | |
| **Treatment** | **9.57** | **1** | **0.023** | **55.947** |
| Territory location | 0.11 | 1 | 0.737 | 57.834 |
| Pup presence | 0.22 | 1 | 0.639 | 57.728 |
| Time of day | 0.52 | 1 | 0.471 | 57.428 |
| | | *Effect Size* | *SE* | |
| Constant | | 1.847 | 0.107 | |
| Group ID | | 0.104 | 0.356 | |
| **(c) Group proportion** | | | | |
| **Treatment** | **9.94** | **1** | **0.019** | **-2.752** |
| Territory location | 3.34 | 1 | 0.068 | -4.088 |
| Pup presence | 1.33 | 1 | 0.249 | -2.081 |
| Time of day | 0.08 | 1 | 0.783 | -0.828 |
| | | *Effect Size* | *SE* | |
| Constant | | 0.708 | 0.066 | |
| Group ID | | 0.141 | 0.18 | |

The analyses used data from four experimental trials run in 13 groups. Presented test statistics for the fixed effects were obtained by running the minimal model against the minimal model including the fixed effect of interest. Effect Size and Standard Error (SE) were extracted from the minimal model: for the Constant, they represent the estimated mean value and the variance around this mean; for the random term (Group ID), they represent the variance and the standard deviation.

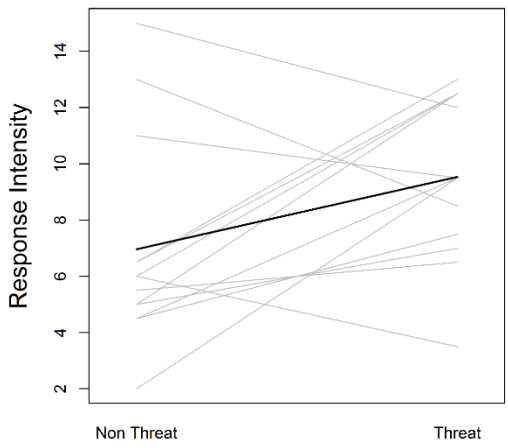
**Table 2.** Linear Mixed Models on factors affecting (a) speed of travel (log transformed), (b) distance travelled (square root transformed), (c) direct distance travelled (square root transformed); (d) travel circuity (log transformed) and (e) area covered (log transformed).

| | $\chi^2$ | *Df* | *P* | *AIC* |
|---|---|---|---|---|
| **(a) Speed** | | | | |
| **Treatment** | **12.78** | **1** | **0.005** | **-16.205** |
| Location | 0.05 | 1 | 0.829 | -14.252 |
| **Pups** | **8.21** | **1** | **0.004** | **-16.205** |
| Time of day | 0.48 | 1 | 0.491 | -14.680 |
| | | *Effect Size* | *SE* | |
| Constant | | -0.649 | 0.062 | |
| Group ID | | <0.001 | 0.151 | |
| **(b) Distance** | | | | |
| **Treatment** | **10.68** | **1** | **0.014** | **193.982** |
| Location | 0.47 | 1 | 0.492 | 195.510 |
| **Pups** | **8.56** | **1** | **0.003** | **193.982** |
| Time of day | 0.75 | 1 | 0.387 | 195.233 |
| | | *Effect Size* | *SE* | |
| Constant | | 13.658 | 1.657 | |
| Group ID | | < 0.001 | 4.028 | |
| **(c) Direct distance** | | | | |
| Treatment | 5.35 | 1 | 0.148 | 175.382 |
| Location | 1.80 | 1 | 0.180 | 174.936 |
| Pups | 0.25 | 1 | 0.617 | 176.483 |
| Time of day | <0.001 | 1 | 0.980 | 176.733 |
| | | *Effect Size* | *SE* | |
| Constant | | 6.302 | 0.646 | |
| Group ID | | 0.703 | 3.309 | |
| **(d) Circuity index** | | | | |
| Treatment | 4.88 | 1 | 0.181 | 60.320 |
| Location | 2.64 | 1 | 0.104 | 58.562 |
| Pups | 0.01 | 1 | 0.909 | 61.188 |
| Time of day | 0.14 | 1 | 0.708 | 61.061 |
| | | *Effect Size* | *SE* | |
| Constant | | 0.979 | 0.09979208 | |
| Group ID | | <0.001 | 0.556 | |
| **(e) Area covered** | | | | |
| Treatment | 3.76 | 1 | 0.288 | 80.764 |
| Location | 0.44 | 1 | 0.509 | 80.090 |
| Pups | 0.14 | 1 | 0.705 | 80.382 |
| Time of day | 0.07 | 1 | 0.795 | 80.458 |
| | | *Effect Size* | *SE* | |
| Constant | | 2.319 | 0.187 | |
| Group ID | | 0.397 | 0.674 | |

The analysis used data from four experimental trials run on eight groups. Presented test statistics for the fixed effects were obtained by running the minimal model against the

minimal model including the fixed effect of interest. The AIC values for two significant fixed effects were extracted from the minimal model including both terms. Effect Size and Standard Error (SE) were extracted from the minimal model: for the Constant they represent the estimated mean value and the variance around this mean; for the random term (Group ID) they represent the variance and the standard deviation.

**Figure 1**


Response Intensity
2
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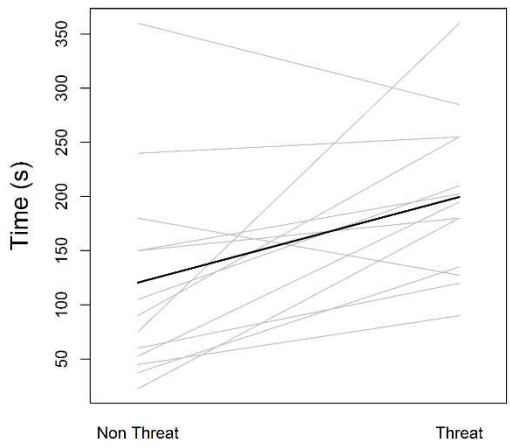
12
14
Non Threat
Threat


Time (s)
50
100
150
200
250
300
350
Non Threat
Threat

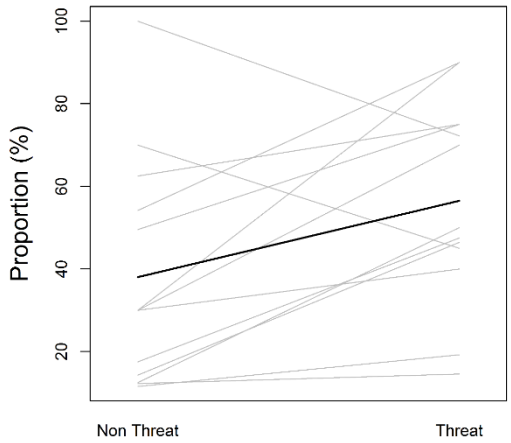
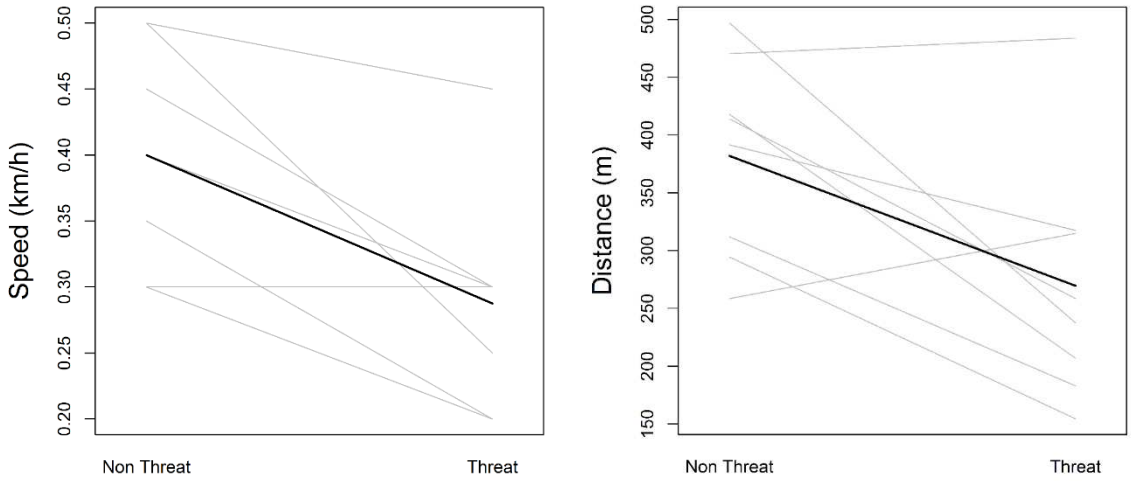

Proportion (%)
20
40
60
80
100
Non Threat
Threat

**Figure 2**


Speed (km/h)
0.20
0.25
0.30
0.35
0.40
0.45
0.50
Non Threat
Threat
Distance (m)
150
200
250
300
350
400
450
500
Non Threat
Threat